

SHORT COMMUNICATION

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Effects of elevated temperature and sedimentation on grazing rates of the green sea urchin: implications for kelp forests exposed to increased sedimentation with climate change

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Abstract

Sea urchin grazing rates can strongly impact kelp bed persistence. Elevated water temperature associated with climate change may increase grazing rates; however, these effects may interact with local stressors such as sedimentation, which may inhibit grazing. In Alaska, glacial melt is increasing with climate change, resulting in higher sedimentation rates, which are often associated with lower grazer abundance and shifts in macroalgal species composition. The short-term effects of elevated temperature and sediment on grazing were investigated for the green sea urchin, *Strongylocentrotus droebachiensis* (O.F. Müller, 1776), in Kachemak Bay, Alaska (59° 37' 45.00" N, 151° 36' 38.40" W) in early May 2017. Feeding assays were conducted at ambient temperature (6.9–9.8 °C) and at 13.8–14.6 °C with no sediment and under a high sediment load. Grazing rates significantly decreased in the presence of sediment, but were not significantly affected by temperature. Along with sediment impacts on settlement and post-settlement survival, grazing inhibition may contribute to the commonly observed pattern of decreased macroinvertebrate grazer abundance in areas of high sedimentation and increased sedimentation in the future may alter sea urchin grazing in kelp forests.

Keywords: Temperature, Sediment, *Strongylocentrotus*, Grazing

Introduction

Kelp forests are critical biogenic habitats distributed along temperate and polar coasts worldwide that support high biodiversity [1]. Sea urchins are frequently the most important consumers within kelp forest communities and exert top-down control on kelp distribution, abundance, and species composition [2]. Loss of urchin predators can lead to phase shifts from kelp forests to urchin barrens [2], alternative stable states with lower productivity and structural complexity than kelp forests [3, 4]. Once formed, urchin barrens can persist for many decades due to continued high urchin densities and destructive grazing inhibiting kelp recovery [5].

Climate change is causing global and local changes in physical conditions which may have significant effects on sea urchins and their role in shaping kelp forests. Global mean sea surface temperature has increased by 1 °C over the last century [6] and is projected to continue increasing with continued fossil fuel use [7]. Marine invertebrate prey consumption rates are predicted to increase with elevated temperature due to increased metabolic rates within their thermal tolerance window [8]. Elevated temperature increases consumption rates of some marine invertebrates including gastropods [9], sea stars [10], and sea urchins [11]. Climate-induced increases in kelp consumption could threaten the persistence of productive kelp forests [12], although decreased herbivory and kelp recovery has also been observed in response to warming [13]. Sedimentation rates have increased or are predicted to increase in several kelp forest systems around

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the world due to changes in land-use or climate change (e.g. New Zealand [14], US Atlantic [15], Europe [16]). At high latitudes, glaciers are melting at accelerating rates [17], resulting in increased glacial discharge that delivers fine sediment to the nearshore environment [18]. As glacial melt increases with increasing air temperatures, the amount of sediment deposited in the nearshore environment could increase, or sediment plumes could spread farther, making these high-sediment conditions more common in kelp forests. In the Arctic, wind-induced water motion during longer ice-free summers has led to increased sediment resuspension [19] and erosion rates are expected to continue accelerating [20]. Sedimentation is an important driver of benthic community structure and can limit grazer abundance near points of glacial discharge in Alaska [21] and other high-sediment locations [22]. Lower grazer survival and/or grazing rates may contribute to this pattern. Sedimentation can scour tissues of invertebrate grazers, and may interfere with movement, attachment to substrate, and gas exchange [22]. Some macroalgae that are palatable to sea urchins (such as *Saccharina latissima*) persist near points of glacial melt despite high sediment loads [21, 23]. Because sedimentation rates are predicted to increase in the nearshore environment [15–17, 24], it is important to know how sedimentation affects urchin grazing rates to anticipate changes in herbivore-plant interactions in the future.

Kelp forest community responses to warming sea temperatures may vary with sediment load. Increased sea temperature may interact with local stressors and alter top-down effects in kelp forest systems in ways that cannot be predicted by studying the effects of global or local stressors alone. In low sediment areas, increased temperature could result in increased kelp consumption by urchins leading to reduced kelp biomass and contributing to the maintenance of urchin barrens [25–27]. High sedimentation may increase urchin energetic costs by reducing grazing efficiency or causing urchins to increase movement [22]. Temperature and sedimentation may have synergistic negative effects on urchins, if grazing rates cannot increase to meet metabolic needs in the presence of sediment. Although elevated temperature and other stressors can affect a wide range of species interactions [28] and other aspects of sea urchin populations such as recruitment and larval survival [29], here I focus on sea urchin grazing on kelp. This study investigated the effects of increased temperature and sediment load on grazing rates of the green sea urchin, *Strongylocentrotus droebachiensis* in Kachemak Bay, Alaska. The experiment tested three hypotheses: (1) grazing rates are higher at predicted temperature for the year 2030 (14 °C, Hadley and Canadian climate models [30]) than ambient temperature (6.9–9.8 °C), (2) grazing rates are lower

under high sediment conditions (1-cm thick layer of fine settled sediment) than without sediment, and (3) under combined conditions of future temperature and high sediment load, grazing rates are higher than those under ambient temperature and high sediment load.

Materials and methods

Sample collections

One adult *Strongylocentrotus droebachiensis* (30–40 mm test diameter, 14.95 g mean wet weight \pm 0.57 SE, n = 36) was used in each treatment. Urchins were collected from 10-m depth mean lower low water (MLLW) from an urchin barren on the northern coast of Kachemak Bay (59° 37' 45.00" N, 151° 36' 38.40" W) on 4/28/2017, transported to the Kasitsna Bay Laboratory and held in a tank with ambient flow-through sea water. While in the holding tank, urchins were fed *Saccharina latissima* collected from the shallow subtidal (2–3 m) at Kasitsna Bay to satiation each day. Urchins were held in the laboratory for 8, 14, or 19 days before the first, second, and third runs of the experiment, respectively. Urchins were then moved to experimental jars (1-L mason jars with mesh-covered openings to allow water exchange) and starved, and the temperature was gradually increased to 14 °C over 2 days in the elevated temperature treatment. Urchins in ambient temperature treatment were also held in experimental jars during this time and were exposed to ambient temperature. This resulted in a starvation period of 2 days for urchins in all treatments. At the start of the grazing trial, ~ 5 g (4.98 ± 0.12 , mean \pm SE, n = 72) of *S. latissima* were added to each jar and weighed down with a small rock, just before sediment was added. Sediment was collected from the shallow subtidal (2–3 m) at Kasitsna Bay, dried and sieved to retain fine sediment < 63 μ m, then 6 g was sprinkled over the top of the jar to distribute it evenly, forming a 1-cm thick layer (1600 mg cm⁻²) in the bottom of the experimental jar at the start of the experiment. This also resulted in a thin film of sediment (< 1-mm thick) on the piece of kelp in the jar.

Experimental design

Two temperature levels (ambient [6.9–9.8 °C] and elevated [14 °C]) and two sediment load levels (no sediment and high (1-cm thick layer)) were manipulated in a crossed design for a total of four treatment combinations (n = 3 per treatment) during three experimental runs (5/6–5/8, 5/12–5/14, and 5/17–5/19/2017). Each treatment had a paired no-urchin control which was used in grazing rate calculations. The elevated temperature level is approximately 2 °C above the average summer high temperature in Kachemak Bay, Alaska (based on average temperature during the warmest 24-h period in each year from 2002 to 2014 [31]) and is the expected summer high

temperature for the year 2030 [32]. The sediment treatments are based on observations of sediment layers on rocks at sites downstream of glacial melt (Traiger pers obs).

In the first two experimental runs, twelve 1-L mason jars were placed in each of two plastic tanks (91 × 41 × 38 cm). One tank contained a tank heater set at 14 °C for the high temperature treatment, while the other tank was the ambient temperature control. Unfiltered seawater was pumped into the laboratory from Kasitsna Bay, flowed into each tank through one hose placed at the center of the tank and flowed out through the top of the tank. Three replicates of sediment treatment jars (six mason jars, half with urchins and half without urchins) were placed in each tank. For the third run, additional heaters became available, so a total of six glass tanks (51 × 30 × 25 cm) were used, three of which contained a heater, with one replicate of each sediment treatment (four mason jars, half of which were no-urchin controls) in each tank. Jars were randomly positioned within all aquaria. Sea water flow rates through each tank were maintained at approximately 20 mL s⁻¹ to allow water circulation throughout the tank, but to prevent sediment from dispersing out of the mason jars for all experimental runs. One Honest Observer by Onset (HOBO) Pendant data logger (Onset Computers, Bourne, Massachusetts) was floated at the surface of each tank and temperature was recorded hourly. Only five loggers were available, so the ambient tank number 5 was randomly selected as the tank for which no temperature data were collected (Table 1). There were three replicates of each of the four treatments (ambient temperature and no sediment, ambient temperature and high sediment, elevated temperature and no sediment, and elevated temperature and high sediment) per experimental run. The jars without urchins are not considered a treatment here because those data were used in the calculation of grazing rates.

After each experiment the remaining *S. latissima* were weighed and feeding rates (mg kelp g urchin⁻¹ h⁻¹) for each replicate were calculated using the formula: $F = [(F_0 - F_t) - (F_{b0} - F_{bt})] / WT$, where F_0 and F_t are the start and end kelp weights with an urchin, F_{b0} and F_{bt} are the start and end weights of kelp in the paired no-urchin control jar, W is the urchin weight, and T is the experiment duration [33].

Statistical analysis

Grazing rates were compared among treatments using a linear mixed effects model (lme4 package [34]) in R Studio version 1.1.456 [35]. Temperature (levels: ambient, elevated) and sediment (levels: no sediment, high sediment) were fixed factors and tank (10 tanks) nested

Table 1 Average temperature (± standard error) in each experimental tank. Only five loggers were available, so the ambient tank 5 was randomly selected as the tank for which no temperature data were collected

Treatment	Average temperature (°C) ± standard error
Ambient	
Run 1, Tank 1	6.86 ± 0.02
Run 2, Tank 3	7.62 ± 0.03
Run 3	
Tank 5	No data
Tank 6	9.76 ± 0.21
Tank 7	8.96 ± 0.18
Elevated	
Run 1, Tank 2	14.65 ± 0.06
Run 2, Tank 4	13.92 ± 0.03
Run 3	
Tank 8	13.89 ± 0.02
Tank 9	13.75 ± 0.02
Tank 10	13.85 ± 0.01

Table 2 Results of a linear mixed effects model testing the effects of temperature and sediment on sea urchin grazing with tank nested within experimental run as a random factor

Source	SS	MS	df	F-value	P-value
Temperature	7465	7465	1	2.217	0.147
Sediment	163,530	163,530	1	48.561	<0.001
Temperature: sediment	8087	8087	1	2.401	0.132

Italics indicates significant P-value (α=0.05)

within experimental run (3 runs) was included as a random factor. Tank was included in the analysis so that any procedural effect of including all replicates within the same tanks in the first two runs could be detected. Residuals plots were visually examined for normality and equal variance.

Results and discussion

Grazing rates were significantly different between the no sediment and high sediment treatments (Table 2, F -value = 48.561, P -value < 0.001) and grazing rates were 89–94% lower in the presence of high sediment (Fig. 1). Although there appeared to be a trend toward higher grazing rates with elevated temperature within no sediment treatments, this was not significant and there was no significant interaction between the sediment and temperature treatments (Table 2). The negative effects of sediment likely overpowered any positive effect of temperature on grazing rates. With a higher sample

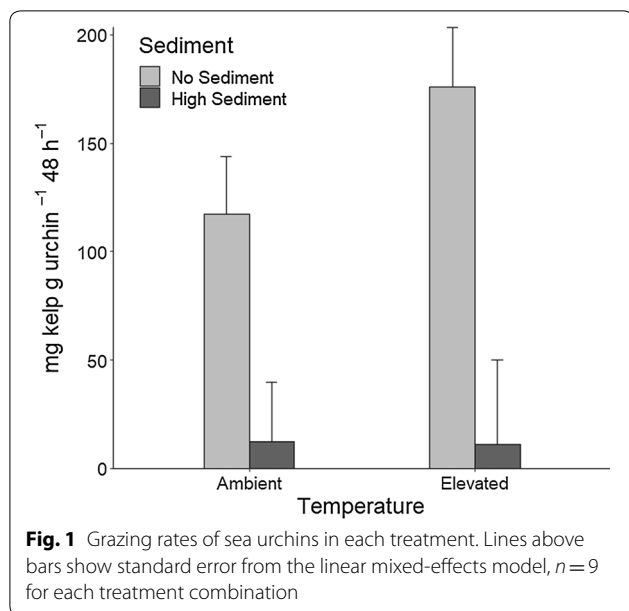


Table 3 Variance and standard deviation associated with the random effects

Random effects	Variance	Standard deviation
Tank: experimental run	<0.001	<0.001
Experimental run	992.6	31.5
Residual	3368.0	58.0

size, a significant interaction between temperature and sediment may have been detected. Grazing rates varied among experimental runs and the highest grazing rates were observed during run 3 in the elevated temperature, no sediment treatment at $251.7 \text{ mg kelp g urchin}^{-1} 48 \text{ h}^{-1}$ ($\pm \text{SE } 54.8$, $n = 3$) (Table 3, Additional file 1: Figure S1). Although urchins were fed to satiation daily until the starvation period, the length of time urchins were held in the laboratory previous to the start of the experiment may have contributed to the variation in grazing rates among experimental runs for the no sediment treatments (Additional file 1: Figure S1). As urchins used in later trials were held in the laboratory longer, they had longer to recover from the stress of collection and this reduced stress may have allowed their grazing to increase compared to earlier trials. Grazing rates below zero during run 2 for the high sediment treatments indicate that kelp in the no-urchin control jars had deteriorated over the course of the grazing trial. Temperature varied among tanks in the ambient treatments from $6.9 \text{ }^\circ\text{C}$ ($\pm \text{SE } 0.019$, $n = 56$) to $9.8 \text{ }^\circ\text{C}$ ($\pm \text{SE } 0.209$, $n = 51$) (Table 1) due to temperature changes in the flow-through seawater source. Temperature of the elevated treatment tanks was

slightly higher in the first run than the remaining runs ($14.6 \text{ }^\circ\text{C} \pm \text{SE } 0.060$, $n = 56$) (Table 1).

There was a significant depression of sea urchin grazing under high sediment load. Sea urchins in the high sediment treatment tended to stay on the sides or top of the experimental jars to avoid the settled sediment, which apparently prevented them from accessing the kelp, which itself was covered with only a thin layer of settled sediment. Sea urchins can survive with low food supplies for extended periods [36], and may be able to adapt to seasonally or temporarily high sedimentation rates by moving to microhabitats with less sediment. Although *Strongylocentrotus droebachiensis* can climb up the stipes of some kelps, such as *Laminaria digitata* [37] to avoid sediment, *Saccharina latissima* in glacially-influenced areas have short, flexible stipes and the blade lies prostrate along the bottom [38], so climbing onto *S. latissima* would not allow urchins to fully avoid sediment. While sediment cover on kelp pieces in this experiment was light compared to the bottom of the jar, sediment cover on the blades of *S. latissima* in nature can be substantial, even burying blades [39]. Lower grazer abundance is commonly observed in locations with high sedimentation, including glacial estuaries [21] and rocky intertidal and subtidal reefs near mining operations [40]. Sediment avoidance and grazing inhibition are potential mechanisms behind this pattern. In Plymouth, UK, experimental laboratory and field studies found that fine sediment inhibited limpet grazing and abundance patterns in the rocky intertidal were related to sediment deposition [41]. Field transplant experiments have shown that scouring and burial by sediments can cause high mortality of adult limpets [42]. Sediment may also limit grazer populations through negative effects on settlement and early life stage survival. For example, sedimentation reduces larval settlement and juvenile survival of the New Zealand urchin, *Evechinus chloroticus* [43]. Sedimentation in coastal vegetated habitats may increase in the future with continued glacial melt [44], increased precipitation [45], and soil erosion [24]. If sedimentation increases in kelp forests, sea urchin grazing pressure may decrease. Changes in macroalgal composition and abundance are likely to occur simultaneously with grazing pressure in response to increase sediment. In Alaska, kelp diversity is typically lower near points of glacial sediment input and the sediment-tolerant *S. latissima* is often the dominant kelp species [21, 46, 47]. Although extreme increases in sedimentation can result in loss of even this sediment-tolerant kelp, as in Norway where sediment deposition from frequent flooding resulted in the loss of 90% of *S. latissima* forests along the southern coast [48]. Although sedimentation affects sea urchin grazing rates, at high sedimentation rates the direct effects of sediment on

macroalgae may be more important in affecting macroalgal composition and abundance.

In contrast to some previous studies, there was not a significant increase in sea urchin grazing rate with elevated temperature. Laboratory and field experiments on urchins in the Galapagos Islands found that increased temperature resulted in stronger top-down effects on algal biomass and sea urchin grazing rates were five times higher during the warm season compared to the cold season [26, 27]. Increased temperature also increases urchin grazing rates on seagrass [49]. In a laboratory experiment in Australia, only small individuals of the urchin, *Heliocidaris erythrogramma*, were able to increase grazing rates to compensate for increased metabolic rate at future predicted temperature [50]. There are distinct differences in consumption rates of kelp recruits by sea urchins and herbivorous fish between warm and cool regions in Portugal [51]. In Norway, feed conversion ratios of juvenile *S. droebachiensis* held at 12 and 14 °C were higher than those at 6 and 10 °C [52]. However, in a short-term (48-h) feeding trial using *S. droebachiensis* from the Gulf of Maine, grazing rates were lower at 20 °C than at 13 or 16.5 °C [53]. Although differences in experimental design (i.e. starvation period, temperature, urchin size) make comparison of grazing rates to other studies difficult, grazing rates in this study seem to be lower than those observed in similar short-term lab experiments with *S. droebachiensis* (~ 1–3 g kelp consumed in [53]; 0.8 g kelp consumed on average in McKay and Heck [54]). *Strongylocentrotus droebachiensis* experience higher temperatures at the southern part of their distribution than the higher temperature treatment used in this study (14 °C), but marine invertebrates like *S. droebachiensis* are often adapted to local temperature regimes [55], so it could still be expected that their grazing rates increase at this temperature. The high temperature treatment used here was approximately 2 °C above mean summer high temperature in Kachemak Bay but a maximum temperature of 13.6 °C was observed in recent years (2002–2014) [31] so *S. droebachiensis* in this area may have started adapting to these high temperatures. While there was not a significant interaction between elevated temperature and high sedimentation on grazing rate in this study, this could change with a more extreme temperature increase. There was a nonsignificant trend towards higher grazing rate at the higher temperature, no sediment treatment, and a significant effect of temperature may have been detected with higher replication. Grazing rates can also vary with season and reproductive status [56], and these factors are beyond the scope of this short-term experiment.

While many studies have been conducted to examine the effects of individual stressors associated with climate change on the survival or growth of individual

species, investigating the impacts of multiple stressors on species interactions is critical to determining ecosystem responses [57, 58]. Changes in environmental conditions which affect marine invertebrate grazing can have cascading effects with consequences for habitat complexity and species abundance and diversity. For example, turfing, foliose, or filamentous macroalgae, which provide less complex habitat than kelps, can persist where the presence of sediments deters grazing [59–61]. This study indicates that grazing suppression by sedimentation may outweigh temperature-driven increases in grazing, at least at the modest temperature increase examined here, although further study with greater replication is needed. While this study was short-term, it indicates that even short-term pulses of sediment may significantly affect urchin grazing. Sedimentation is a dynamic process that is expected to change in many nearshore ecosystems and it is important to understand how these changes will interact with global changes in temperature to affect the role of grazers in coastal vegetated habitats. This study supports the hypothesis that sedimentation inhibits invertebrate grazing in high-sediment environments where macroalgae can persist, and illustrates the importance of considering such local stressors in the study of the effects of climate change on nearshore systems.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s10152-019-0526-x>.

Additional file 1: Figure S1. Grazing rates of sea urchins in each treatment and experimental run (figure legend). Lines above bars show standard error, $n = 3$ for each treatment in each experimental run. Grazing rates below zero during run 2 for the high sediment treatments indicate that kelp in the no-urchin control jars had deteriorated over the course of the grazing trial.

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Authors' contributions

I am the sole author of this manuscript. The author read and approved the final manuscript.

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Availability of data and materials

The datasets used during the current study are available from the corresponding author on request.

Ethics approval and consent to participate

Sea urchins and kelp were collected with permission of the State of Alaska Department of Fish and Game (Permit Number CF-17-069). No human subjects or vertebrate animals were used in this study.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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